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# Woody encroachment slows decomposition and termite activity in an African savanna

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## Abstract

Woody encroachment can lead to a complete switch from open habitats to dense thickets, and has the potential to greatly alter the biodiversity and ecological functioning of grassy ecosystems across the globe. Plant litter decomposition is a critical ecosystem process fundamental to nutrient cycling and global carbon dynamics, yet little is known about how woody encroachment might alter this process. We compared grass decay rates of heavily encroached areas with adjacent nonencroached open areas in a semi-arid South African savanna using litterbags that allowed or excluded invertebrates. We also assessed the effect of woody encroachment on the activity of termites— dominant decomposer organisms in savanna systems. We found a significant reduction in decomposition rates within encroached areas, with litter taking twice as long to decay compared with open savanna areas. Moreover, invertebrates were more influential on grass decomposition in open areas and termite activity was substantially lower in encroached areas, particularly during the dry season when activity levels were reduced to almost zero. Our results suggest that woody encroachment created an unfavourable environment for invertebrates, and termites in particular, leading to decreased decomposition rates in these areas. We provide the first quantification of woody encroachment altering the functioning of African savanna ecosystems through the slowing of aboveground plant decomposition. Woody encroachment is intensifying across the globe, and our results suggest that substantial changes to the carbon balance and biodiversity of grassy biomes could occur.

**KEYWORDS**
bush encroachment, *Dichrostachys cinerea*, global change, litterbags, Macrotermitinae, naphthalene, nutrient cycle, soil fauna, Termitoidae, woody thickening

## 1 | INTRODUCTION

Woody plant cover is increasing in grassy systems around the world, converting once open areas into dense thickets (Asner, Elmore, Olander, Martin, & Harris, 2004; Parr, Gray, & Bond, 2012; Stevens, Lehmann, Murphy, & Durigan, 2017). African savannas, which cover approximately 13.5 million square kilometres (Riggio et al., 2013), are no exception to this woody encroachment (also known as woody thickening) that has been documented since the early 20th century (Bews, 1917), but has become increasingly prevalent over the last several decades (Archer, Boutton, & Hibbard, 2000; O'Connor, Puttick, & Hoffman, 2014; Wigley, Bond, & Hoffman, 2010). While poor land management (e.g. overstocking), changes in land use practices and changes in fire regimes can promote woody encroachment, global drivers such as increased atmospheric concentration of carbon dioxide that favours the growth of C3 woody plants over C4 grasses

  

are also likely to be influential (Archer, Schimel, & Holland, 1995; Stevens, Erasmus, Archiblad, & Bond, 2016; Wigley et al., 2010).

Initially viewed as a threat to agriculture, woody encroachment occurs across multiple land uses, and in some instances protected areas have had the highest rates of encroachment (O'Connor et al., 2014; Stevens et al., 2017; Wigley et al., 2010). A shift from grass- to woody-dominance in savannas reduces grazing capacity for herbivores, and results in cascading ecosystem effects (Eldridge et al., 2011; Parr et al., 2012; Sirami, Seymour, Midgley, & Barnard, 2009). The induced ecosystem changes are often highly variable, with effects largely dependent on the species of encroaching woody plant (Eldridge et al., 2011). Nonetheless, woody encroachment affects grassy biomes across the globe, and its prevalence is predicted to intensify in the coming decades (Moncrieff, Scheiter, Bond, & Higgins, 2014; Stevens et al., 2017). Potential changes to ecosystem function from woody encroachment therefore warrant research attention and understanding, especially given the antiquity, high biodiversity value and carbon sequestration potential of grassy systems (Bond & Parr, 2010; Grace, Jose, Meir, Miranda, & Montes, 2006; Parr, Lehmann, Bond, Hoffmann, & Anderson, 2014).

Plant litter decomposition is a major ecological process linked to nutrient cycling and carbon dynamics (Raich & Schlesinger, 1992). Rates of decay are controlled by various agents, such as biotic activity (e.g. termites and fungi) and UV radiation, and drivers that regulate the influence of these agents (e.g. climate and litter quality) (García-Palacios, Maestre, Kattge, & Wall, 2013; Hobbie, 1992; Wardle et al., 2004). To-date, only a handful of studies, all restricted to North American drylands, have assessed how woody encroachment might affect decomposition (Hewins, Sinsabaugh, Archer, & Throop, 2017; Throop, Abu Salem, & Whitford, 2017; Throop & Archer, 2007), with differences in decomposition rates largely attributed to alterations in abiotic controls, such as soil-litter mixing and solar radiation. However, the influence of woody encroachment on the decomposer community and their effects on decomposition remains unknown. Moreover, understanding of the effects of woody encroachment on decomposition in other systems is required before broad consensus can be reached.

Here, we investigate plant litter decomposition in a semi-arid African savanna with high levels of encroachment by an indigenous woody plant, *Dichrostachys cinerea* ((L.) Wight & Arn), which occurs over large areas of southern Africa (Bester, 1999; O'Connor et al., 2014; Roques, O'Connor, & Watkinson, 2001). We examine: (i) the effects of woody encroachment on the rate of aboveground grass decomposition, (ii) the contribution of invertebrates to plant litter decomposition in open and encroached areas, and (iii) the effect of encroachment on the diversity and activity of fungus-growing termites, highly influential decomposers in African savannas (Buxton, 1981; Collins, 1981; Freymann, Buitenwerf, & DeSouza, 2008). We predicted that decomposition would be slower in encroached areas because the increased dominance of a single woody plant species at the expense of herbaceous undergrowth would reduce the activity of decomposer organisms through reduced food diversity and altered microclimatic conditions. In addition, the increased shade (canopy cover) resulting from woody encroachment was anticipated to reduce UV radiation, thereby decreasing photodegradation and slowing decomposition (Austin, 2011; Austin & Vivanco, 2006).

## 2 | MATERIALS AND METHODS

### 2.1 | Study site

The study was conducted in Madikwe Game Reserve, South Africa (24°47′S; 26°10′E), a semi-arid savanna that receives approximately 540 mm of rain per year, typically falling between October and March. Substantial encroachment, often at the expense of grasses, has been documented in this system (Symeonakis & Higginbottom, 2014), with a 30% increase in woody cover (predominantly by *D. cinerea*) recorded in Madikwe between 1955 and 1996 (Hudak & Wessman, 2001).

We established 20 experimental replicates (50 × 50 m plots, spaced >100 m apart to ensure independence) in encroached areas in the south of the park, and 20 replicates in open savanna areas in close proximity. The encroached areas consisted of patches of woody encroachment set within a matrix of non-encroached, open savanna. Ten of the open savanna replicates were placed in an adjacent area, up to 3 km from the encroached sites, and another ten were placed further away, up to 18 km from the encroached sites, within a fenced area due to concerns that wildlife would damage litterbags in the exposed, open savanna sites over the 12 month experimental period (See Table S1 for additional study site information). The dominant historical land use across the study area, including the experimental replicate sites, was cattle grazing, with <5% of the area used for cropping (Hudak & Wessman, 2001). We made use of historical aerial photographs (dating back to 1955) to confirm that the selected sites (encroached and open) did not differ in their historical land use (e.g. agriculture vs cattle ranching). To quantify any other potential differences in local environmental variables between the open and encroached areas, we measured the following attributes within each replicate: (i) percentage cover of bare ground, grass, forbs, dead wood and woody plant canopy; (ii) grass species composition; (iii) soil depth and (iv) soil texture. Percentage cover of each attribute in (i) was estimated in nine 1 × 1 m quadrats per experimental replicate, each spaced 10 m apart, using a five-point scoring system (1 = <5%, 2 = 5%–25%, 3 = 26%–50%, 4 = 51%–75%, 5 = 76%–100%) and estimating the total percentage cover with the following equation:

$$\text{Total percentage cover} = \sum \frac{\text{midpoint \% for a score value} \times \text{no. quadrats with that score value}}{\text{total no. quadrats}} \quad (1)$$

Annual temperature and precipitation data for each replicate were obtained from WorldClim – Global Climate Data (Fick & Hijmans, 2017) online resource at a 30 s spatial resolution (http://worldclim.org/bioclim). Grass species were identified at 50 points, spaced 1 m apart, diagonally across each replicate following

the step-point method (Evans & Love, 1957). Soil depth was measured using a 300 mm peg that was hammered into the ground at four points spaced >25 m apart in each replicate. This relatively shallow maximum soil depth (300 mm) was chosen because it was considered the most critical for termite activity, with most termites foraging within the first 250 mm of soil (Wood, 1988; Wood, Johnson, Bacchus, Shittu, & Anderson, 1982). A soil sample was also collected at each of these four points with a soil auger to a standardised depth of 20 cm. Soil samples were pooled per plot and a 50 g subsample was used to determine soil texture (sand, silt, and clay content) with a particle size analysis using the pipette method (Briggs, 1977). We buried iButtons® (Thermochron, Maxim/Dallas Semiconductor Corporation, Dallas, TX, USA) 2 cm below the soil surface in three replicates in each area (open and encroached) to measure hourly soil temperature for the duration of the study.

## 2.2 | Decomposition experiment

We filled aluminium gauze litterbags with 9 g of *Themeda triandra* (Forssk.), oven dried at 70°C for 48 hr. *Themeda triandra* was chosen because it is a common, widespread local grass species with relatively high palatability (Van Oudtshoorn, 1999) and has been used previously in savanna decomposition experiments (e.g. Davies, van Rensburg, Eggleton, & Parr, 2013), where it decomposed at a rate that was expected to yield differences in mass loss between treatments over the course of our 1 year experiment. The litterbags measured 15 × 15 cm and consisted of 2 × 2 mm mesh (following Davies, van Rensburg, et al., 2013), allowing access by most small- to medium-sized invertebrates, including termites.

Each experimental replicate had two sets of litterbags, spaced 10 m apart: a treatment that suppressed invertebrates and a control (no invertebrate suppression). Naphthalene, an arthropod repellent, was used to suppress invertebrates and was chosen to avoid the problems of altered microclimates associated with litterbags of different mesh sizes (Bradford, Tordoff, Eggers, Jones, & Newington, 2002). Naphthalene is commonly used in decomposition studies (Austin & Vivanco, 2006; Powers et al., 2009; Wall et al., 2008) and provides a conservative estimate of the faunal contribution to litter decomposition (Blair, Crossley, & Rider, 1989). Two naphthalene balls (approximately 8 g each) were placed underneath each treatment litterbag and replaced every 2 months to ensure sustained invertebrate suppression. In July 2013, six litterbags were nailed directly onto the substrate at each treatment and control set. One litterbag was collected from each litterbag set every 2 months for 1 year, starting in September 2013 (2 months in the field) and ending in July 2014 (12 months in the field). A total of 480 litterbags were used in the experiment: 2 savanna habitats (open and encroached) × 20 replicates each × 2 treatment sets each (control and invertebrate suppression) × 6 sampling periods. After collection, litterbags were oven dried at 70°C for 48 hr. Litter was then hand-sorted to remove any soil and weighed to determine proportional mass loss (grass mass remaining was subtracted from the initial mass of each bag).

## 2.3 | Termite activity

Cellulose baits (single ply, unscented toilet rolls) were used to measure termite activity within the open and encroached areas during 2 × 4-monthly periods, roughly spanning the wet (November 2013–March 2014) and dry (March 2014–July 2014) seasons. Nine baits were placed at each replicate, arranged in a 3 × 3 grid with 10 m spacing, with the first line of baits positioned 10 m from the decomposition experiment. We used two measures of termite activity: i) the amount of bait consumed, and ii) the frequency with which baits were attacked. Bait consumption was visually estimated after 2 and 4 months in each season according to the percentage consumed, following Davies, Eggleton, van Rensburg, and Parr (2013): 0 = 0%; 1 = 1%–25%, 2 = 26%–50%, 3 = 51%–75%, 4 = 76%–99%, 5 = 100%. For consistency, bait consumption was scored by the same observer throughout the study. Baits that had a consumption score of ≥2 after 2 months were replaced with new ones to ensure continuous bait availability. A cumulative score for each season (wet and dry) was calculated by either summing the two scores for the season if a bait had been replaced (i.e. maximum score = 10), or using the score after 4 months if a bait had not been replaced (i.e. maximum score = 5). Therefore, the cumulative consumption score for each season ranged from 0 (0% of the baits consumed) to 10 (100% of the baits consumed). Since termites have the potential to consume more bait than was provided, consumption scores of 10 (100% of both baits consumed over the 4-month period) could be considered as a conservative estimate of termite activity levels. However, this possibility does not apply to our specific study because full consumption of both baits did not occur in any replicate (see Results). The frequency of termite attack at baits, measured as the proportion of baits per grid ($n$ = 9) that showed signs of termite consumption, was also recorded every 2 months.

The experiment was reset after the wet season to measure termite activity during the dry season. To avoid spatial autocorrelation, a new grid of fresh baits was placed on the opposite side of the litterbags, 30 m away from the original grid, and the same scoring procedure followed. Termites present at baits were collected and stored in 70% ethanol for later identification, using the soldier caste and following Uys (2002). The number of baits per replicate within which a particular termite species was encountered served as a measure of relative abundance (Davies, Eggleton, et al., 2013). As an additional measure of termite activity in open and encroached areas, we recorded the number of termites present in litterbags collected in January, the peak of the summer wet season when savanna termites are most active (Davies, Eggleton, van Rensburg, & Parr, 2015).

## 2.4 | Data Analysis

We constructed multiple generalised linear mixed effects models with binomial error distributions to assess the effect of habitat (encroached or open), treatment (control or invertebrate suppression), sampling period (month), and aggregated termite activity (bait consumption across seasons) on the proportional mass loss (hereafter,

mass loss) from litterbags. Analysis of litterbag mass loss after 12 months between the open sites that were close to the woody encroached areas and those that were further away revealed no significant differences (Mann-Whitney *U*-test, W = 31, $p = .15$). We therefore did not distinguish between these different open savanna sites in subsequent analyses. The experimental replicate was set as a random effect in all models to account for each litterbag set within a replicate being repeatedly sampled over the six collection events. Candidate models, consisting of all combinations of fixed effects and their first and second order interactions, were compared using sample size-corrected Akaike's Information Criterion (AICc), and the model with the lowest AICc value (hereafter, best model) was used for further analysis using a Type II Analysis of Deviance test (Wald Chi-square test) to assess effect size and significance of each predictor variable and interaction term present in the model (Crawley, 2007). The performance of the best model was assessed for goodness of fit, homogeneity of variance and normality of residuals. Analyses were performed using the *lme4* package in R software, version 3.3.3 (R Core Team, 2016).

Litterbags collected after 12 months were used to estimate the decomposition constant (k), for each habitat (encroached or open) and treatment (control or invertebrate suppression), using the negative exponential single-pool decomposition model (Olson, 1963):

$$W_t = W_0\, e^{-kt} \tag{2}$$

where $W_0$ is the initial litter mass (time = 0 years) and $W_t$ is the litter mass after collection (time = 1 year).

Although k only describes average decomposition rates over 1 year and is likely to change over time, it is useful for comparison between habitats and treatments. The constant k (/year) was then used to estimate the half-life of grass material following (Olson, 1963):

$$T_{0.5} = \frac{0.693}{\mathrm{k}} \tag{3}$$

where *T* is litter half-life and k is the decomposition constant calculated from Equation 2.

Mann-Whitney *U*-tests were applied to the percentage cover and soil depth data to compare environmental variables between habitats, as well as termite activity between habitats and seasons. Soil texture was compared between habitats using Student's *t*-tests (percentage sand, silt and clay content). Soil texture data were first arcsine transformed to meet the assumptions of normality. Mean monthly minimum and maximum soil temperatures were analysed using a linear mixed effects model, with experimental replicate set as the random effect (repeated measure) to account for measurements being recorded continuously from the same locations over the experimental year.

To assess whether there was a relationship between litterbag mass loss and termite activity (bait consumption as well as frequency of attack), linear regressions were performed for each habitat using the mass lost from control litterbags collected after 12 months and the average yearly termite activity scores (calculated from the wet and dry season bait consumption and frequency of attack per replicate). In addition, we regressed termite bait consumption scores against the frequency of termite occurrence at each habitat to assess how termite bait consumption was related to termite presence. Finally, an analysis of similarity (ANOSIM) was performed using PRIMER software v.5.0 (Clarke & Warwick, 2001) to assess whether the termite and grass communities differed between habitats.

## 3 | RESULTS

Open savanna areas had more grass cover than encroached areas, which in turn had more dead wood and greater woody plant canopy cover (Table 1). Although mean soil depth was greater in open areas (Table 1), there was considerable overlap with soil depth values in the encroached sites (Figures S2 and S3). Bare ground, forb cover and soil texture (sand, silt and clay content) did not differ between open and encroached areas (Table 1), and there were no significant differences between grass assemblages in encroached and open sites (Global $R = 0.11$, $p = .06$). Monthly soil temperatures were higher in open savannas (Table 1), largely due to significantly higher mean maximum temperatures than encroached areas (Figure S1). In addition, the open savanna had more extreme soil temperatures, with the lowest and highest recorded temperatures (−2.5°C and 69°C, respectively) exceeding those of encroached areas (1.5°C and 58°C, respectively). Open and encroached sites showed little difference in annual air temperature (mean ± standard error, open savanna: 20.30 ± 0.06°C; encroached: 20.41 ± 0.01°C) and annual precipitation (mean ± standard error, open savanna: 537.10 ± 2.51 mm; encroached: 538.25 ± 1.28 mm) (see also Table S1).

### 3.1 | Decomposition rates

Grass litter in the open savanna decomposed twice as fast (half-life ($T_{0.5}$) of control litterbags = 1.23 ± 0.37 years) as that in encroached areas ($T_{0.5}$ = 2.49 ± 0.26 years) (Figure 1). Differences in litterbag mass loss over time varied between open and encroached areas (there was a significant interaction between habitat and sampling period, Tables S2 and S3, Supplemental material), with similar losses observed during the first 6 months (the dry season), but mass loss being faster in the open savanna in the second 6 months, corresponding with the wet season months (Figure 1).

Invertebrates increased decomposition rate in both open and encroached areas, with control litterbags losing more mass than those that excluded invertebrates (Figure 1). However, invertebrates were more influential in the open savanna where their suppression resulted in a greater decrease in decomposition rates relative to their suppression in the encroached areas (Table 2).

Termite activity influenced litterbag mass loss across habitats and seasons (Table S1), but was more influential in open savannas during the wet season, as indicated by the significant two-way interactions between termite activity and habitat, as well as termite

**TABLE 1** Environmental variables measured at open and encroached savanna areas in Madikwe Game Reserve, South Africa

| | Environmental variable | Open savanna | Woody encroached | Test statistic | *p*-Value |
|---|---|---|---|---|---|
| Total percentage cover | Bare ground | 65.69 | 64.79 | 65,670.00[a] | .77 |
| | Grass | 17.59 | 11.56 | 105.00[a] | <.05* |
| | Forbs | 3.62 | 3.61 | 149.50[a] | .13 |
| | Dead wood | 3.522 | 6.07 | 312.00[a] | <.01* |
| | Canopy cover | 5.61 | 14.76 | 266.00[a] | <.05* |
| Mean values | Soil depth (mm) | 229.38 | 167.96 | 4,424.00[a] | <.01* |
| | Sand (%) | 83.85 | 81.7 | −1.31[b] | .20 |
| | Coarse silt (%) | 13.10 | 15.7 | 1.60[b] | .12 |
| | Medium/fine silt (%) | 2.30 | 1.55 | −1.30[b] | .20 |
| | Clay (%) | 0.75 | 1.05 | 1.44[b] | .16 |
| | Soil temperature (°C) | 23.23 | 22.13 | 2.36[c] | <.05* |

Total percentage cover (calculated using Equation 1, see Methods) are presented for variables scored according to their percentage cover in nine quadrats in each of 20 experimental replicates per habitat (open and encroached). Mean values are presented for the other variables. Test statistics are from Mann-Whitney *U*-tests[a], Student *t*-tests[b] or the β coefficients from a linear mixed effects model[c]. Significant ($p < .05$) differences between treatments are denoted with an asterisk.

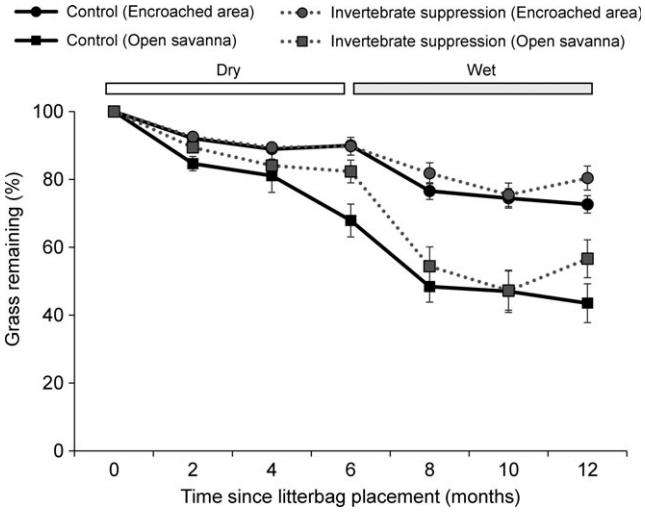


**FIGURE 1** Mean (±standard error) percentage grass mass remaining in litterbags collected over 12 months in open and encroached savanna areas in Madikwe Game Reserve, South Africa. Litterbags either allowed (control) or suppressed invertebrates (treatment). Wet and dry season months are indicated above the figure

activity and sampling period (Figure 2a; Table S2). The increase in litter mass at the final collection event (Figure 1) could either be an artefact of individual variation in litterbag decomposition rates (a common occurrence in sacrificial litterbag sampling protocols) or be due to tightly adhered soil particles and/or microbial biomass collected over time.

## 3.2 | Termite activity and species composition

Termite activity was significantly greater in open savannas (frequency of attack = 86%; median intensity of attack = 2.61) compared with encroached areas (frequency of attack = 60%; median intensity of attack = 1.81, $p < .01$), and was higher during the wet season at both open and encroached areas (Figure 3). There was a significant relationship between bait consumption (across seasons) and litterbag mass loss after 12 months in encroached areas (Figure 2a), but not in the open savanna. In contrast, there was a significant relationship between the frequency of termite occurrence and litterbag mass loss (Figure 2b), as well as between bait consumption and frequency of termite occurrence in the open savanna, but not in the encroached areas (Figure 2b,c).

**TABLE 2** Decomposition constants (k/year) for litterbag treatments that allowed invertebrates (controls, denoted as +Invert) or suppressed invertebrate activity (treatment, denoted as −Invert) in open and encroached savanna areas in Madikwe Game Reserve, South Africa

| Habitat | + Invert | − Invert | Δk |
|---|---|---|---|
| Open savanna | 0.95 | 0.65 | 0.30 |
| Woody encroached | 0.33 | 0.23 | 0.10 |

We sampled termites from more baits in the open savanna ($n = 100$) than the encroached areas ($n = 41$). In addition, termites were only found in litterbags sampled in the open savanna ($n = 12$ litterbags) during the wet season, with control litterbags containing more termites ($n = 70$) than naphthalene treated litterbags ($n = 33$). Six termite genera were sampled, with their relative abundances differing between habitats and seasons, being generally higher in the open savanna and during the wet season (Figure 4). Due to clear morphological differences in the *Odontotermes* soldier caste, we were able to separate this genus into three distinct morphospecies. This was not possible for other genera. However, differences in termite assemblages between open and encroached areas were small (ANOSIM, Global $R = 0.13$, $p < .01$), and no species turnover was observed: genera were simply sampled at lower abundances in encroached areas (Figure 4). *Allodontermes* and *Odontotermes* were

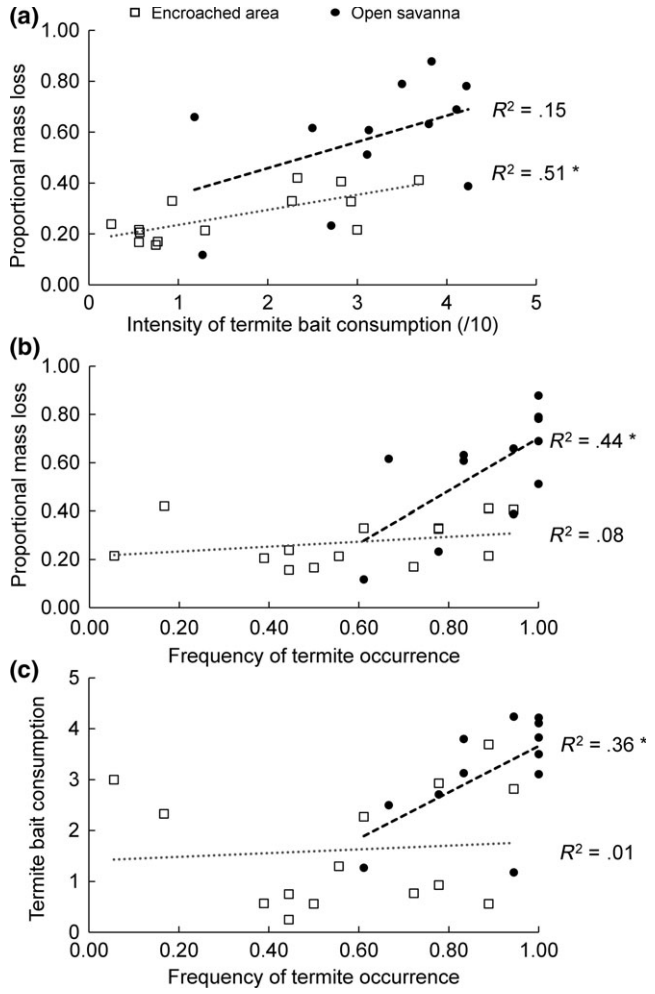


**FIGURE 2** Proportional mass loss measured from control litterbags (invertebrates not suppressed) in relation to termite bait consumption (a), frequency of termite attack at baits (b), and bait consumption by termites in relation to the frequency of termite occurrence (c) 12 months after litterbag placement in encroached and open savanna areas in Madikwe Game Reserve, South Africa. Linear regression lines for the best fitting model are added (encroached area: black; open savanna: grey). Significant regressions are indicated with an asterisk. Termite consumption was scored from cellulose baits on a scale of 0 (no bait consumption) to 10 (total bait consumption). Frequency of attack was measured as the proportion of baits per experimental replicate that showed signs of termite activity

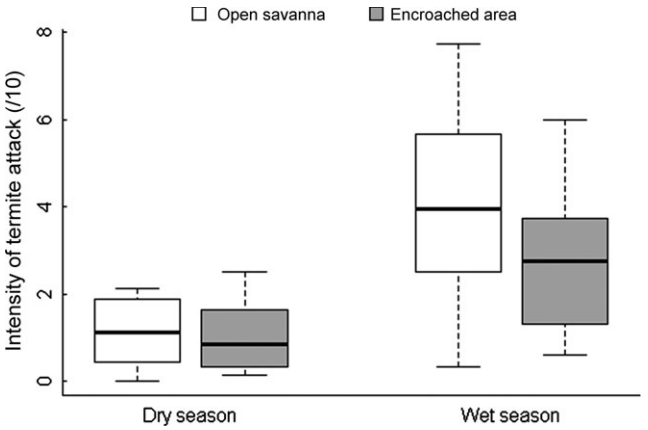


**FIGURE 3** Boxplots indicating median (central line within box), interquartile range (box) and extreme (whiskers) termite activity scores (measured as the intensity of termite attack at cellulose baits) in open and encroached savanna areas in Madikwe Game Reserve, South Africa. Cellulose baits were scored according to the percentage of bait consumed by termites on a scale from 0 (no consumption) to 10 (total consumption) during the dry and wet season

the only genera that were more abundant during the dry season, and this was only true for the open savanna (Figure 4).

## 4 | DISCUSSION

Our results reveal substantial differences in aboveground litter decomposition rates and termite activity between open and encroached savanna areas, suggesting that woody encroachment can affect the functioning of savanna ecosystems. Encroached areas had significantly slower rates of decomposition, and we suggest that the decline in fungus-growing termite activity in these areas was likely a key determinant of this pattern. That changes in the termite community are a strong driver of changes in decomposition rate is supported by both the reduced number of termites sampled in encroached areas, and by the slower decomposition rates when invertebrates were suppressed. Slower decomposition in encroached areas has important implications for the global carbon budget, given the importance of decomposition to global carbon fluxes (Raich & Schlesinger, 1992), as well as for nutrient cycling in these systems. The reduction in termite activity in encroached areas also has important implications for multiple other ecosystem processes since termites are keystone organisms that influence several attributes of savanna ecosystems, including soil properties, hydrology, vegetation communities and the patterns and impacts of herbivory (Davies et al., 2016; Joseph et al., 2015; Sileshi, Arshad, Konate, & Nkunika, 2010).

Slower decomposition under woody encroachment corroborates previous findings from a North American dryland (Throop & Archer, 2007), and suggests that this phenomenon is more widespread, extending to African savannas. Slower decomposition under woody encroachment also supports the notion that encroachment will likely lead to substantial changes in the functioning of grassy ecosystems (Parr et al., 2014; Scholes & Archer, 1997), especially since woody encroachment is predicted to intensify in the future (Grace et al., 2006; Moncrieff et al., 2014). These changes have implications for future carbon dynamics since carbon will remain on the surface longer where decomposition is slower. However, slower decomposition may not necessarily lead to greater carbon storage in encroached areas because the inhibition of the grass-layer and associated fine-root biomass can decrease local carbon storage potential (Coetsee, Gray, Wakeling, Wigley, & Bond, 2013; Hudak, Wessman, & Seastedt, 2003).

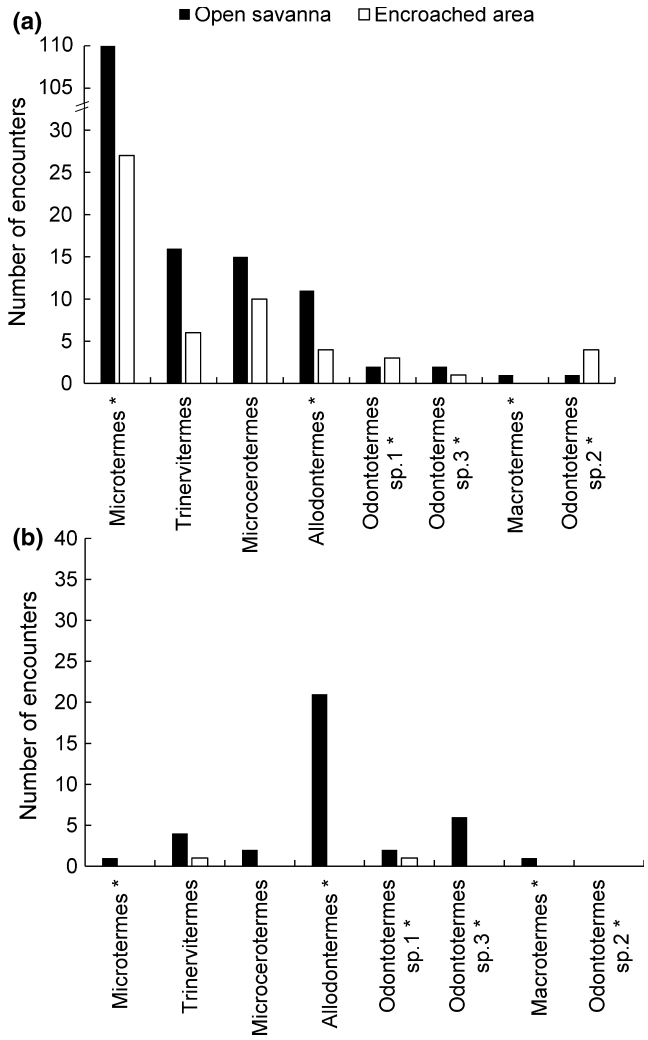


**FIGURE 4** Number of encounters of each termite genus (and morphospecies in the case of *Odontotermes*) sampled from cellulose baits during the wet (a) and dry (b) season in Madikwe Game Reserve, South Africa. *Odontotermes* were separated into three morphospecies due to clear morphological differences in the soldier caste. Termite genera/morphospecies are ranked according to their abundance in open savanna areas during the wet season. Fungus-growing termite genera are denoted with an asterisk

Throop and Archer (2007) suggested that decreases in decomposition rates under woody encroachment were due to a reduction in soil-litter mixing because of increased grass cover under woody shrubs (although the mechanism for this remains unclear). In contrast, we found less grass cover in the encroached areas, suggesting that increased woody plant density reduces, rather than increases, herbaceous undergrowth in African savannas (Parr et al., 2012; Scholes & Archer, 1997; Symeonakis & Higginbottom, 2014). An alternative mechanism is therefore likely driving differences in decomposition under encroachment in our system, and we suggest that the reduced activity of fungus-growing termites in encroached areas is a key driver.

While encroached areas might be expected to provide favourable habitat for termites due to increased canopy cover and woody plant abundance that provides increased UV protection and buffering of extreme soil temperatures (Figure S1), as well as an increase in the availability of dead wood, which serves as a food source for termites (Eggleton et al., 1996; Jones et al., 2003; Muvengwi, Mbiba, Ndagurwa, Nyamadzawo, & Nhokovedzo, 2017), termite abundance was lower in encroached areas. Termite abundance in the encroached areas could be lower because the encroaching woody species, *D. cinerea*, is suggested to be a poor food source for termites: it is frequently used in house construction and for fence posts due to its resistance to termite attack (Arbonnier, 2004; Brokensha, Warren, & Werner, 1980). The traits of woody encroaching species (e.g. their palatability to decomposers) have been emphasised previously (Eldridge et al., 2011), and could affect the nature and degree of the impact of encroachment on ecosystems.

While it is also possible that the generally shallower soils in the encroached areas represent suboptimal habitat for fungus-growing termites, savanna termites generally forage close to the soil surface (top 25 cm; Wood, 1988). In addition, deeper soils were not consistently associated with higher termite activity (Figure S2), and it is unlikely that soil depth was the primary cause of differences in decomposition rates between open and encroached areas, although our limited number of depth measurements means this finding should be treated with some caution.

Decomposition rates in both habitats also varied temporally, increasing substantially after 6 months of field placement, which coincided with the onset of the summer rains. Furthermore, termite activity affected decomposition rates through its interactions with both season and habitat, being most influential in the open savanna during the wet season. This is not surprising given the role of climate in influencing decomposition rates (Lavelle et al., 1993), and because savanna termites are more active during the wet season (Davies et al., 2015) Seasonal effects therefore warrant consideration in decomposition studies, as opposed to only considering annual variation in climate, particularly in seasonally varied environments such as savannas.

A greater frequency of termite encounters was a significant predictor of enhanced litter mass loss and bait consumption in open savanna (Figure 2b,c). However, in encroached areas, high frequency of termite attack did not translate into greater bait consumption (Figure 2c). This finding is likely due to the low number of encounters (relative abundance) of fungus-growing termite species in encroached areas (Figure 4). Although we were unable to quantify this fully, fewer individuals may have consumed each bait in encroached areas (explaining the low intensity of attack values) even when the frequency of baits attacked per replicate was high. These results show that to predict decomposition rates, it is not enough to simply know how frequently termites attack baits (as was the case for the open savanna), but also to quantify the amount of bait consumed.

The nonsignificant relationship between litterbag mass loss and termite consumption rates in the open savanna (Figure 2a) suggests that termites are not the sole drivers of decomposition in this system. Photodegradation is an important agent of decomposition in arid environments (Austin, 2011; Austin & Vivanco, 2006), and has been shown to enhance plant litter decomposition in our study site

(Leitner, 2015). It is therefore likely that in addition to direct negative effects on termites, woody encroachment also reduces the amount of photodegradation due to increased canopy cover, further contributing to slower decomposition rates. Further testing of the relative roles of invertebrates and photodegradation in African savannas, including those undergoing woody encroachment, are needed before the contribution of each driver is fully understood. Similarly, while we observed woody encroachment to slow rates of grass litter decomposition, the potential effects of encroachment on wood decomposition remain to be investigated (but see Leitner, 2015), particularly as wood becomes the dominant litter type in encroached areas, and is likely to have even greater implications for the carbon budgets of these areas.

Nevertheless, our results suggest that woody encroachment has the potential to substantially alter aboveground litter decomposition and termite activity in African savannas. These findings have important and broadly applicable implications for ecosystem functioning given the vast expanse of savannas across Africa (>13 million square kilometres (Riggio et al., 2013), the importance of decomposition for biogeochemical cycling and the global carbon budget (Raich & Schlesinger, 1992), as well as termites being a keystone taxon increasing soil productivity and landscape heterogeneity (Jouquet, Tavernier, Abbadie, & Lepage, 2005; Sileshi et al., 2010). Such changes to ecosystem processes and biodiversity resulting from current levels of woody encroachment should be adequately considered in predictions of global change impacts because they could challenge our understanding of how grassy systems function.

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## DATA ACCESSIBILITY

Data used in this manuscript have been archived in Figshare https://figshare.com/s/ba48395035371ccde16b.

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## SUPPORTING INFORMATION

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